ICES CM 2008/C:14 Not to be cited without prior reference to the authors

Length structure of deep-pelagic fishes sheds new light to their life histories

Mikko Heino, David S. Boukal, Tone Falkenhaug, Uwe Piatkowski, Filipe M. Porteiro and Tracey T. Sutton

Here we use a new technique to study life history variation in deep-pelagic fishes from a mid-ocean ridge system. Shape of length distribution in a population is to a significant extent determined by the degree to which an average individual approaches its asymptotic maximum size. Analysing the material from the pelagic trawl hauls taken during the 2004 Mar-Eco expedition along the northern Mid-Atlantic Ridge, we show that length distributions in many deep-pelagic fish species are characterised by negative skew (the left tail of the distribution is longer). In other words, a large proportion of individuals had a size close to species-specific maximum size. Provided that our sampling can be considered representative, this finding suggests that deep-pelagic fishes have a low mortality rate relative to the rate at which they grow towards their asymptotic size.

Keywords: Life history, growth trajectory, mortality

M. Heino (corresponding author): Department of Biology, University of Bergen, Box 7800, N-5020 Bergen, Norway, and Institute of Marine Research, Bergen, Norway, and International Institute for Applied Systems Analysis, Laxenburg, Austria. Tel.: +47 55584544, fax: +47 55584450, e-mail: mikko.heino@bio.uib.no.

D. Boukal: Institute of Marine Research, Box 1870 Nordnes, N-5817 Bergen, and Department of Biology, University of Bergen, Box 7800, N-5020 Bergen, Norway.

T. Falkenhaug: Institute of Marine Research, Flødevigen Marine Research Station, N-4817, His, Norway.

U. Piatkowski: Leibniz Institute of Marine Sciences, IFM-GEOMAR, Düsternbrooker Weg 20, D-24105 Kiel, Germany.

F. Porteiro: Department of Oceanography and Fisheries, University of the Azores, PT-9901-862 Horta, Portugal.

T Sutton: Virginia Institute of Marine Science (VIMS), P.O. Box 1346, Gloucester Point, VA 23062, USA.

Introduction

Ideally, we would like to know everything of each sampled individual, or perhaps at least the 'standard' measurements, say age, length, total weight, sex and maturity. The reality is quite different. Obtaining any individual-level measurement is relatively time-consuming, and often all that is routinely recorded at individual-level is length and perhaps weight. With deepwater fish these difficulties are aggravated: in relatively aseasonal environments, aging becomes increasingly difficult, and very few species can be aged with routine methods. Maturity staging is difficult when background information on reproductive cycles is lacking. Not surprisingly then, despite technological advances at other observation fronts, individual-level data from most fish sampled during the G. O. Sars expedition to the northern Mid-Atlantic Ridge in June–July 2004 are restricted to length (see Wenneck *et al.* 2008 for details).

Length distributions contain information on mortality and growth

What can we learn from length data alone? This is a challenge that fisheries scientists have faced since the twilight years during the first half of the 20th century. Consequently, there is a

long tradition for using length-based methods to study population dynamics and parameters (e.g., Beverton and Holt 1956, Pauly and Morgan 1987, Gulland and Rosenberg 1992). One interesting result concerns the determination of a population's length distribution (Wetherall *et al.* 1987, p. 54). If population-level growth is described by the von Bertalanffy model (with parameters k and l_∞, respectively growth coefficient and asymptotic length), mortality m is constant (at least within the considered length range), and reproduction is continuous, population's length distribution as a probability density distribution yields

$$p_{obs}(l) \sim m/k\,(l_\infty - l)^{m/k-1} / l_\infty^{m/k}. \qquad (1)$$

The shape of the length distribution is determined by the ratio m/k alone, whereas l_∞ is only influencing its horizontal width. Moreover, the length distribution is monotonically decreasing if $m/k>1$ and monotonically increasing in the opposite case. Notice also that because both m and k are expressed in the same unit (time^{-1}), their ratio is a dimensionless number. Thus, we do not need to know the exact value of these two variables, only their ratio, to predict the length distribution. A corollary is that a length distribution alone can give an estimate of the ratio m/k, but not of m and k separately.

Even though the result of Wetherall *et al.* (1987) has been around for more than two decades, the implications of equation (1) seem to have been overlooked: $m/k>1$ leads to a length distribution with a positive skew, which is qualitatively from a positive skew that follows from $m/k<1$.

We have elsewhere (Heino *et al.* 2008) preliminarily shown that the correspondence between the skew coefficient and the ratio m/k is not only qualitative but also quantitative. Furthermore, this result seems to be robust to assumptions about observability (small individuals evade typical sampling methods), no growth variability (we allowed l_∞ to be a Gaussian deviate) and size-independent mortality (results not shown in Heino *et al.* 2008). Skewness can thus be used to estimate the ratio m/k.

Skew in length distributions of deep-pelagic fish

We have estimated the skewness coefficient for deep-pelagic fishes collected during measured the 2004 G. O. Sars expedition to the northern Mid-Atlantic Ridge. Only a small proportion of individuals were measured, but we assume that what was representative. Data from all trawl hauls with a single gear (smallish macro-zooplankton trawl with uniform meshes (6 mm stretched) or a medium-sized pelagic trawl with graded meshes (22 mm stretched in codend)) are combined, assuming that each haul was equally representative. A population's length distribution is thus estimated as the mean of normalized haul-specific length distribution. We then calculate skew using the moment-based estimate, $\frac{1}{n}\sum_i (x_i - \bar{x})^3 / \sigma^3$, where $\bar{x}$ is the mean and σ is the standard deviation of observations.

Results show that deep-pelagic fishes from the Mid-Atlantic Ridge display a continuum of skewness coefficients, with negative values being slightly more frequent than positive ones. The estimates do not seem to depend much on the gear used. There is significant variability within the family with most species represented here, the lanternfishes (Myctophidae).

The large proportion of species with negative skew is unusual relative to the expectation. A preliminary analysis of data from a completely different area (near Greenland) suggests that our findings from the Mid-Atlantic Ridge may not be atypical for deep-pelagic fish (Fig. 2).

For comparison, we show also data from other nekton than fish (Fig. 3). Length distributions for the common cephalopods, cnidarians and crustaceans are overwhelmingly dominated by a positive skew. This suggests that the patterns we see are taxon-specific and not simply sampling artefacts.

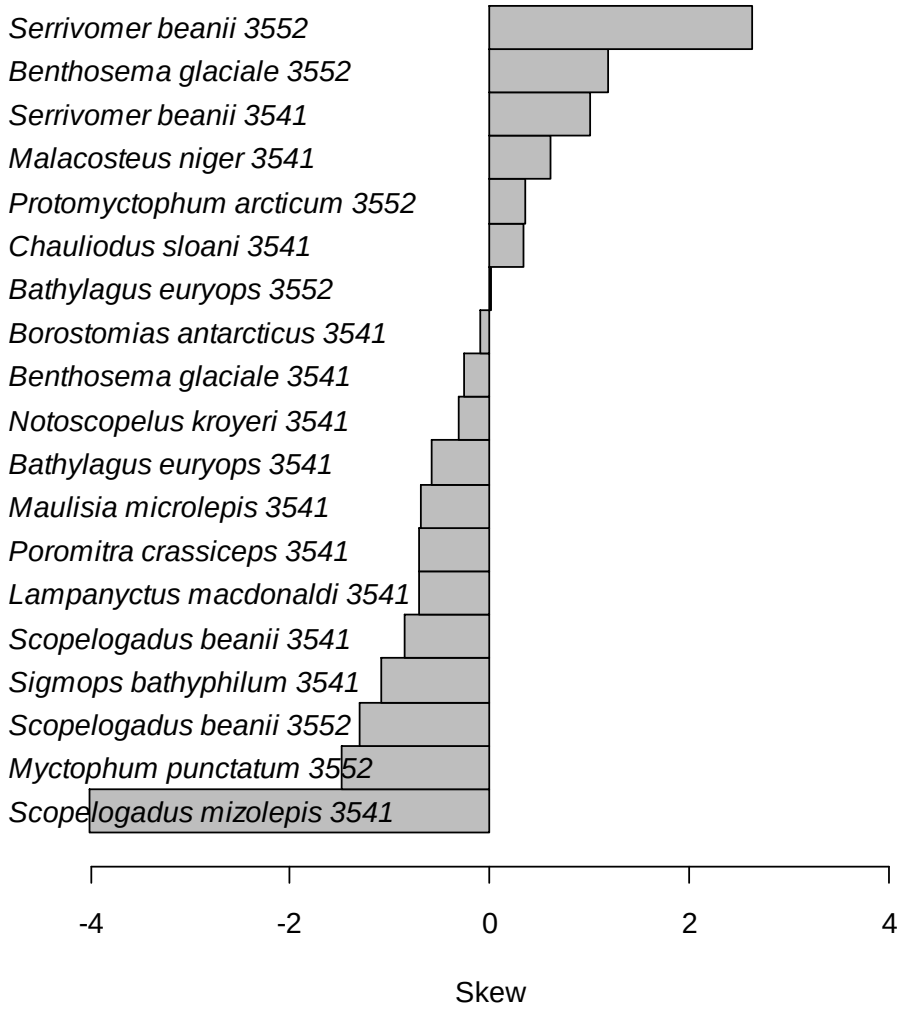

Figure 1. Skewness coefficient for 15 deep-pelagic fish species from the 2004 G. O. Sars expedition to the northern Mid-Atlantic Ridge. The number after species name refers to trawl type (medium-sized pelagic trawl: 3541; small macro-zooplankton trawl: 3552).

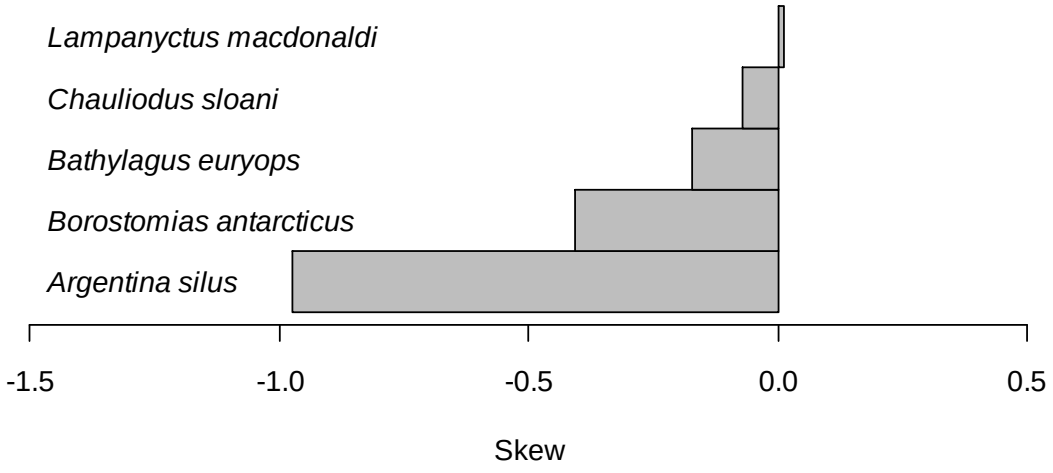

Figure 2. Skewness coefficient for five deep-pelagic fish species from Greenland (data from IFM-GEOMAR, Kiel).

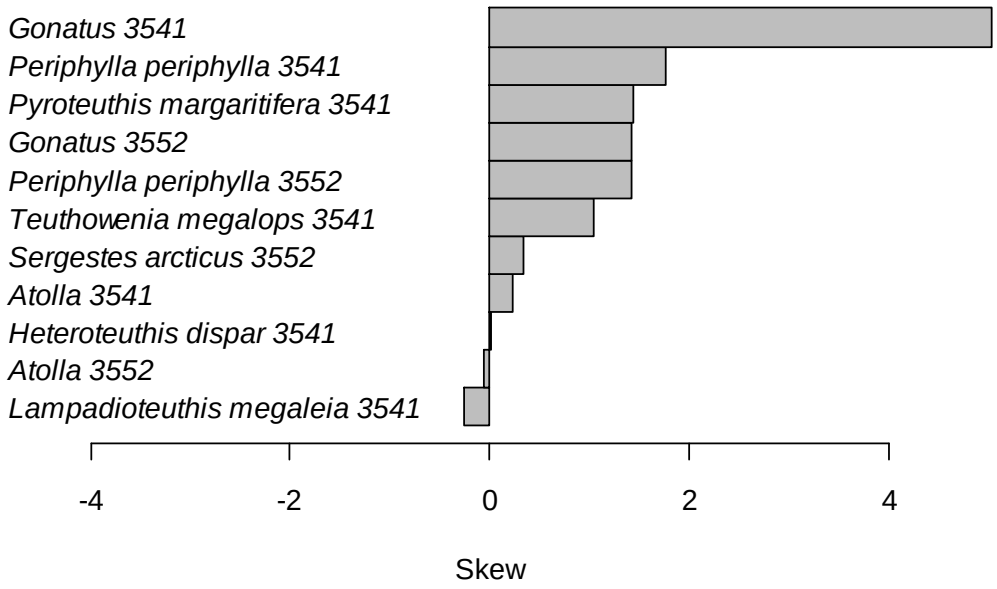

Figure 3. Skewness coefficient for deep-pelagic cnidarians (2 species), cephalopods (5 species) and crustaceans (1 species) from the 2004 G. O. Sars expedition to the northern Mid-Atlantic Ridge.

Discussion

Length distributions with positive and negative skew represent different life history types. When $m/k < 1$ (negative skew), many individuals spend a relatively short proportion of their life span as 'small' individuals, and reach a size that is close to the asymptotic size. In contrast,

when $m/k > 1$ (positive skew), most individuals never reach a large size, and very few individuals get close to the asymptotic size. Length distributions suggest that deep-pelagic fishes span this whole range of life history diversity.

Ratio m/k is also one of the Beverton and Holt (1959) life history 'invariants' or 'statics' that are sometimes assumed to be relatively constant within taxonomic groups (Charnov 1993). For fish, m/k of about 1.5 has been proposed as the canonical value (Charnov 1993), based on the data reported by Pauly (1980) and supported by a simple life history model (Jensen 1996); this 'truth' has then been reiterated elsewhere. $m/k > 1$ should lead to a length distribution with positive skew, *i.e.*, long right tail. This matches perfectly with our idea how 'typical' fish length distributions should look like. However, even a cursory look on Pauly's (1980) data shows that while most populations indeed have $m/k > 1$, there are also many exceptions. There should be many populations with length distributions with a negative skew, or the estimates are inaccurate. However, our results suggest a more systematic deviation from the norm: among deep-pelagic fishes, length distributions with negative skew are dominating.

Our results depend on representativeness of our sampling. However, our analyses so far suggest that skewness is a robustly estimable property that is not easily influenced by size-dependent observability. However, it is entirely possible that we missed some specific components of populations because sampling was confined in space and time. The fishing gears used are selective, and this may also influence our results. Furthermore, we have not yet analysed how non-continuous recruitment influences the skew.

Concluding remarks

Our results shed light to life history diversity among deep-pelagic fishes from the Mid-Atlantic Ridge, of which virtually nothing is known. Studying the skewness of their length distributions suggests that a large proportion of species grow fast relative to their mortality. Or the other way round, they have low mortality relative to their growth. This is in contrast to the usual idea, shaped by shallow-water fishes, that fish length distributions are positively skewed.

References

Beverton, R.J.H. & Holt, S.J. (1956). A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. Rapports et Proces-Verbaux des Reunions du Conseil International pour l'Exploration de la Mer 140, 67-83.

Beverton, R.J.H. & Holt, S.J. (1959). A review of the lifespans and mortality rates of fish in nature and their relation to growth and other physiological characteristics. CIBA Foundation Colloquia on Ageing 5, 142–177.

Charnov, E. (1993). Life history invariants. Oxford University Press, New York.

Gulland, J.A. & Rosenberg, A.A. (1992). A review of length-based approaches to assessing fish stocks. FAO Fisheries Technical Paper. No. 323. Rome, FAO. 100p.

Heino, M., D.S. Boukal, T. Falkenhaug, U. Piatkowski, F.M. Porteiro & T.T. Sutton (2008). Size structure, age-size dynamics and life history variation. ICES CM 2008/F:13.

Jensen, A.L. (1996). Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences 53, 820-822.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. Journal du Conseil International pour l'Exploration de la Mer 39, 175-192.

Pauly D. & G.R. Morgan, eds. (1987). Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.

Wenneck, T. de L., Falkenhaug, T. & Bergstad, O.A. 2008. Strategies, methods, and technologies adopted on the R.V. G.O. Sars MAR-ECO expedition to the Mid-Atlantic Ridge in 2004. Deep-Sea Research II, 55: 6–28.

Wetherall, J.A., J.J. Polovina & S. Ralston (1987). Estimating growth and mortality in steady-state fish stocks from length-frequency data. In Pauly D. and G.R. Morgan (eds.). Length-based methods in fisheries research. ICLARM Conf. Proc., 13:53–74.